Habitat fidelity and habitat utilization of an arboreal mammal (*Myoxus glis*) in two different forests

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Abstract

In a long term study (1982–1994) nest box occupation by edible dormice was investigated in a deciduous and a coniferous-mixed forest. Within both forests edible dormice showed preference as well as avoidance of certain areas. Habitat fidelity was high since shifts between the forests (distance 1 km) was rare. Nest box fidelity was high as well, although higher for females and their daughters than for their sons, and higher in the deciduous, optimal forest than in the coniferous, suboptimal forest. In either forest nest box occupation was correlated with 19 habitat parameters on two spatial scales (900 m^2 and 8100 m^2 around each nest box). These correlations differed considerably between the forests but resulted in a similar interpretation: On the large scale, parameters associated with food availability (e. g. beeches, oaks) and predator avoidance (e. g. tree density, height of the nest box) were important for habitat utilization. On the small scale, habitat choice is less important.

Introduction

Animals live in environments, in which survival and successful reproduction is most likely guaranteed (e. g. Ims 1987; Ostfeld 1990). Their choice of habitats involves responses to patch structure at a series of hierarchical levels and one must consider more than a single scale of patchiness to understand its consequences (Hutto 1985; Wiens 1985; Morris 1987). Thus, it is important to consider spatial scale in studies of habitat associations because the various factors that affect a species may act at different spatial scales (Maurer 1985; Wiens 1986; Bock 1987; Kotliar and Wiens 1990; Orians and Wittenberger 1991; Lima and Zollner 1996).

The edible dormouse (*Myoxus glis* (L.)) is regarded as a species with widespread habitat demands. In Central Europe it is found from park-like landscapes to dense, mixed forests with coniferous and deciduous trees (Storch 1978; Bitz 1990). In general, preferred habitats are deciduous forests with oak trees and other hardwood species. In such habitats dormice show maximized reproductive success and have reached highest population densities (Storch 1978). In this study we investigate whether or not habitat utilization in edible dormice takes place at all and if so, on which spatial scale such a possible choice is made. In contrast to terrestrial voles and mice, arboreal edible dormice are somewhat more difficult to study. Fortunately, besides natural tree holes edible dormice also use artificial nest boxes for resting and rearing their young (see for example Löhrl 1955; v. Vietinghoff-Riesch 1960; Pilastro et al. 1994; Bieber 1995; Schlund 1996).

On two experimentally created scales, nest box occupation frequency of edible dormice was correlated with habitat parameters that were assumed to be important for maxi-

mizing fitness or reproductive success. The small scale encompasses the area directly around a nest box. Here, factors connected with the suitability of the rearing situation such as microclimate or the defendability of the rearing site might be important but also factors that affect survival like the ease of access to the nest box or exposure to predators. The large scale comprises an area that is approximately the size of the mean home range of edible dormice (Hönel 1991). Thus, in addition to the former factors, food availability and presence of competitors and predators at the feeding sites might be important. The described two scales are investigated within two separate forests of different general quality characteristics that influence morphology, survival, and reproduction of edible dormice (Schlund 1996). Insight into the processes of habitat selection can be gained by comparing patterns of habitat utilization by a single species in two habitats that differ in structure (Holmes 1981; Robinson and Holmes 1982). Furthermore, investigating scale effects allows us to distinguish choice hierarchies (Wiens et al. 1987) and thus broaden our understanding of mechanisms determining habitat utilization.

Material and methods

In a 13 year study (1982–1994) we recorded nest box occupation of edible dormice in two woodlands, a deciduous forest of approximately 8 hectars and a coniferous-mixed forest of about 12 hectars. The deciduous forest consists mainly of up to 150 year old tall beech and oak trees (70:20; 10% other tree species; forest management practice for tall branchless tree trunks), and a separate young tree stand with oak, beech and pine trees. The coniferous-mixed forest is more homogeneous with approximately 100 year old pine, spruce and beech trees (60:20:20) and with intermixed 20 year old spruce and beech trees (30:70). Both woodlands are located 1 km from each other within a forest area of 150 km² near Tübingen in south-west Germany (48°33′N, 9°00′E) (see Schlund et al. 1993). Nest boxes were spaced in a 30 m grid in both forests. Some of the nest boxes had small entry holes of 26 mm diameter that were not usable by edible dormice. Thus, only 80 of 88 (in the deciduous forest) and 91 of 124 (in the coniferous-mixed forest) nest boxes were suitable for occupation by edible dormice.

Nest box occupation was determined with the help of the typical leaf nests that are made for resting or giving birth and rearing young. Therefore nest box occupation does not reflect the real number of edible dormice because several animals may live in the nest box at the same time and in the course of a year.

In an area of 30×30 m around each nest box 19 habitat parameters were recorded: Number of trees (DBH > 7.5 cm) of the following tree species: beech *Fagus sylvatica* (BEE), oak *Quercus robur* and *Q. petraea* (OAK), pine *Pinus sylvestris* (PIN), spruce *Picea abies* (SPR), larch *Larix decidua* (LAR), other deciduous trees (OTR) like ash *Fraxinus excelsior*, lime *Tilia platyphyllos* or maple *Acer* sp. and fruit trees (FRT) like apple tree *Malus domestica*, pear tree *Pyrus communis* or cherry tree *Prunus avium*.

DIV: tree species diversity (Shannon-index; Mühlenberg 1989).
DEN: tree density per 30 x 30 m area.
AGE: age of the tree stand, estimated in five classes.
UST: understory cover (e. g. blackberry *Rubus fruticosus* and raspberry *Rubus idaeus*) [m²].
YTR: number of young trees (DBH < 7.5 cm).
TST: number of tree stumps.
HDG: area of the forest edge with hedges [m²].
OPA: open areas (without tree stands; e. g. farmland, meadow or paths) [m²].
HIG: height of the nest box [cm].
CIR: circumference of the nest box tree measured at breast height [cm].
DIS: distance between the nest box tree and the nearest tree with DBH > 30 cm [m].
SUN: measurement of light influx during a 24 h period on top of the nest boxes using an ozalid light meter (Friend 1961; Glück 1979).

For further details see Schlund (1996). Statistical analysis was performed according to Sachs (1984) using the SAS (1987) software package for personal computers.

The two forests differed significantly in most habitat parameters (Tab. 1). Since many of the habitat parameters were highly correlated with each other, we additionally performed a Principal Component

Table 1. Means ($\bar{x}$) and standard deviations (s) of the habitat parameters of the studied areas. Comparison of the habitat parameters between the coniferous-mixed and the deciduous forest (Mann-Whitney-U-test (MWU); z-values and levels of significance (adjusted by applying the sequential Bonferroni test) are given with * = p < 0.05; ** = p < 0.01 and *** = p < 0.001, n = number of investigated grids). Abbreviations see Material and methods.

	deciduous forest $\bar{x} \pm s$ n = 88	coniferous-mixed forest $\bar{x} \pm s$ n = 124	MWU z	p
BEE	33.7 ± 17.4	17.9 ± 8.9	6.72	***
OAK	9.9 ± 8.7	0.1 ± 0.5	12.79	***
PIN	6.8 ± 12.0	13.5 ± 5.5	7.28	***
SPR	–	11.8 ± 8.7	–	–
LAR	1.5 ± 4.2	0.3 ± 0.7	0.62	n.s.
OTR	8.0 ± 18.7	0.4 ± 1.4	6.85	***
FRT	0.4 ± 1.0	0.0 ± 0.2	4.93	***
DIV	0.8 ± 0.3	1.0 ± 0.2	6.15	**
DEN	60.3 ± 26.1	44.0 ± 8.8	5.02	***
AGE	3.6 ± 1.1	4.2 ± 0.6	3.29	**
UST	4.1 ± 17.8	77.6 ± 113.9	6.95	***
YTR	12.1 ± 29.5	39.8 ± 39.0	9.19	**
TST	19.9 ± 11.2	20.1 ± 6.3	1.38	n.s.
HDG	12.1 ± 29.5	2.1 ± 11.6	3.01	**
OPA	10.1 ± 23.9	32.0 ± 54.4	3.37	**
HIG	310.7 ± 25.3	279.6 ± 28.9	8.15	***
CIR	84.8 ± 28.5	101.2 ± 37.4	3.21	**
DIS	2.4 ± 0.7	3.0 ± 1.4	6.45	***
SUN	4.8 ± 0.9	6.2 ± 0.4	7.31	***

Analysis (PCA) on the 19 parameters. Here, as well, the two investigated areas were clearly separated (Fig. 1). The deciduous forest was quite inhomogeneous with mainly old beech and oak trees and with young dense parts of the forest, with diverse tree stands, whereas the coniferous-mixed forest was very homogeneous with pine, spruce and beech trees of similar age.

Occupation frequency of nest boxes was standardized to the number of nest boxes per hectar in each study area. Both forests were then compared with respect to occupation frequency in those 13 years. Absolute differences (t-test for paired samples) as well as the correlation of the course of occupation frequencies between the two study areas were determined.

Two scales were experimentally created and analyzed in order to investigate which factors may play an important role in habitat use of edible dormice. In the small scale analysis the habitat parameters of every 30 × 30 m area (900 m^2) around each nest box were correlated (Spearman rank correlation) with occupation frequency over the 13 years in that central nest box. Correlations were considered significant if they corresponded to p < 0.05 after applying the sequential Bonferroni test (Rice 1989). In addition, we performed a Principal Component Analysis (PCA) on the parameters. A maximum of five axes were computed so that approximately two thirds of the variation was accounted for. These components
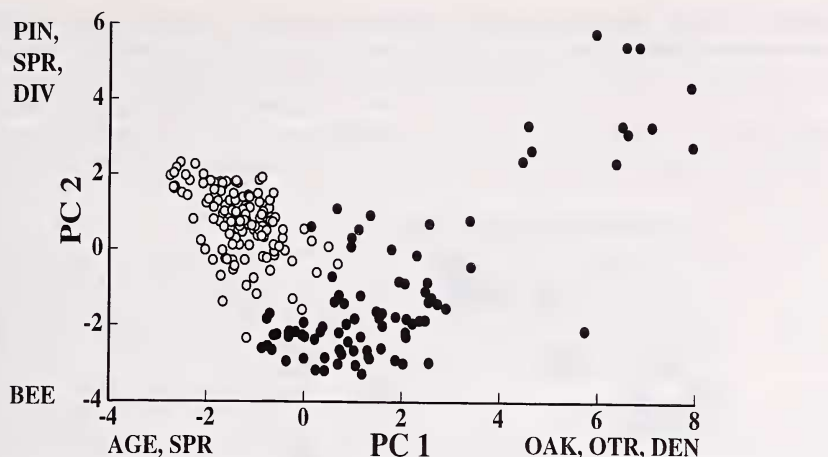
Fig. 1. Distribution of 171 nest box areas in a habitat space defined by the first two components of a PCA based on 19 habitat parameters; (●) deciduous forest, (○) coniferous-mixed forest.

were correlated with occupation frequency. In a separate analysis preference for nest box tree species as well as associated nest box parameters like diameter, height of the nest box and distance to the nearest tree were investigated with respect to occupation frequency. The large scale enclosing the area of 9 nest boxes (90 × 90 m = 8 100 m^2) corresponds to the mean territory size of edible dormice (HÖNEL 1991). Naturally, nest boxes situated at the edge of the study areas had fewer neighbouring nest boxes. There-fore we recorded the 19 habitat parameters for the corresponding 30 × 30 m adjacent areas (without nest boxes) to complete the 90 × 90 m area.

Occupation shifted frequently between adjacent nest boxes from year to year, therefore mean occu-pation frequency of all 9 nest boxes (or correspondingly fewer if nest boxes were not suitable for occu-pation or not present at the edges) was correlated with the mean habitat measurements of the 90 × 90 m area (significant correlations corresponding to p < 0.05 after applying the sequential Bonfer-roni test). In addition, mean occupation rate of the 9 adjacent nest boxes reveals more clearly whether an area was suited for rearing young than just the occupation frequency of the central nest box. Again a PCA was performed and the components were correlated with occupation frequency. The large scale en-compasses the areas of 9 nest boxes but is referred to the corresponding central nest box. This enabled us to analyze both scales with equal sample sizes. As a consequence 6 of the 9 nest box areas overlap with every neighbouring large scale area.

In habitats differing considerably in vegetation structure choice might be made on a non-linear ba-sis (e. g. WIENS 1992) or even in opposite directions. The distance between both woodlands is about 1 km (within a continuous forest) and since exchange between the investigated areas was extremely rare, the two woodlands were analyzed separately and choice patterns were subsequently compared.

In 1993 through 1995 nest boxes were checked once a week between May and October. Dormice were marked individually with passive integrated transponders (SCHLUND 1995), aged, weighed and sexed. Results of this study concerning morphology, population dynamics and reproduction are pre-sented elsewhere (SCHLUND and SCHARFE 1996). By using individual marking nest box constancy and home range fidelity of single dormice could be determined. Also nest box choice of females and subse-quently of their offspring was monitored for several years. The year 1995 was not used for habitat pre-ference analysis because selective logging took place in the winter 1994/1995, thus altering habitat structure considerably.

Results

Occupation frequencies in the 13 years (Fig. 2) were not random and differed from a Poisson distribution in both forests (Chi-square goodness of fit test: $\chi^2 = 304.61$, df = 8, p < 0.001 and $\chi^2 = 379.37$, df = 8, p < 0.001 for the coniferous-mixed forest and deciduous forest, respec-

tively). The Index of Dispersion (ID; Ludwig and Reynolds 1988) indicated clumping (coniferous-mixed forest: ID = 4.08; deciduous forest: ID = 3.95). This shows that differential habitat occupation within both woodlands is due to non random processes.

The density of occupied nest boxes varied considerably throughout the 13 years in both forests ranging from 1.1 to 4.7 occupied nest boxes per hectar in the coniferous-mixed forest and from 0.8 to 4.0 per hectar in the deciduous forest (Fig. 3). The mean oc-
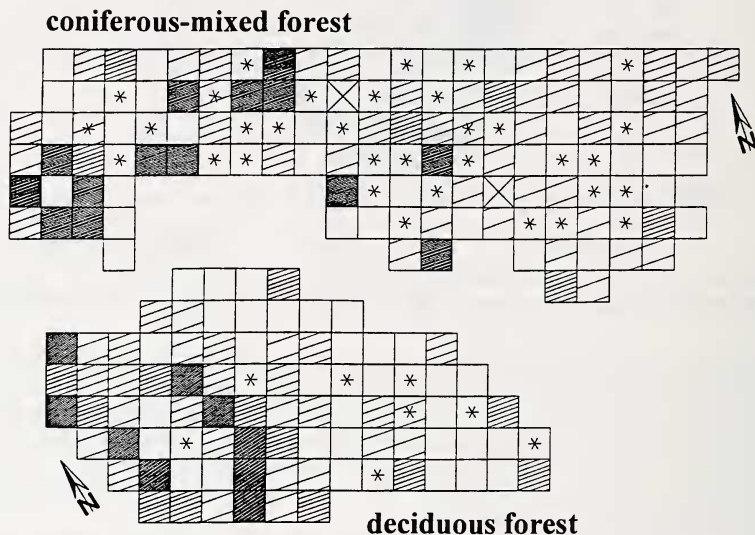
coniferous-mixed forest

deciduous forest

Fig. 2. Occupation frequency of nest boxes by edible dormice from 1982 to 1994 in the deciduous forest (n = 80 suitable nest boxes) and the coniferous forest (n = 91 suitable nest boxes). The nest boxes are spaced in a 30 m-grid.
☐ = no occupation, ◹ = 1–3 occupations, ◩ = 4–6 occupations, ◪ = 7–9 occupations, ■ = > 10 occupations. ✳ = nest box with hole ≤26 mm, ⊠ = area without nest box.
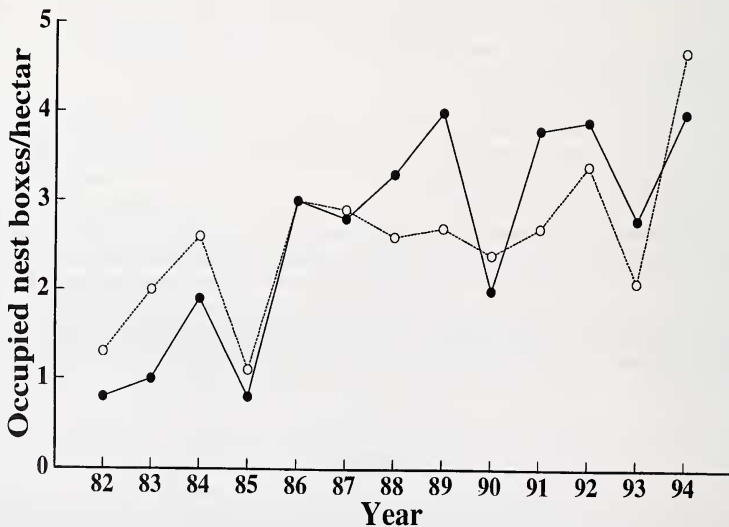

Fig. 3. Number of occupied nest boxes per ha from 1982 through 1994 in the deciduous (●) and coniferous-mixed forest (○).

cupation density did not differ between both habitats (t-test for paired samples: $t = 0.22$, $df = 12$, n. s.), and the course of occupation frequency in the 13 years correlated between the coniferous-mixed forest and the deciduous forest ($r_s = 0.83$, $df = 12$, $p < 0.001$).

Small scale; coniferous-mixed forest:

In the coniferous-mixed forest no significant correlation between nest box occupation frequency and the 19 habitat parameters was found (Tab. 2). Similarly, there was no significant correlation between nest box occupation and any of the PC-axes. 40 out of 91 nest box trees were beeches (44%), pine and spruce trees represented 31% and 24%, respectively. Nest boxes on beeches were occupied significantly above mean occupation frequency, whereas nest boxes on spruce trees were avoided (Fig. 4). The height of the nest boxes attached to beeches correlated positively with occupation frequency ($r_s = 0.42$, $N = 40$, $p < 0.008$). Height of the nest boxes attached to spruce and pine, however, did not correlate significantly ($r_s = 0.07$ and -0.25, respectively).

Large scale; coniferous-mixed forest:

Correlation of the large scale habitat variables with mean occupation frequency of the central nest box and its surrounding 8 nest boxes revealed a significant preference for nest boxes at greater heights with large circumference and a negative correlation with understory cover and tree stumps (Tab. 2).

The first 5 PC-axes accounted for 70.0% of the variation. The significant axes correlating with occupation frequency are shown in figure 4. Correlation with the second axis (accounting for 14.7% of the variation) described a significant positive association ($p < 0.03$) for beech trees and avoidance of understory cover and sun exposure. The fifth axis (only 8.3%) revealed the preference for nest boxes at greater heights and sun exposure ($p < 0.0001$).

Table 2. Spearman rank correlations between the 19 habitat parameters and the occupation frequency of edible dormice for both the small and the large scale of the investigated forests. Levels of significance were adjusted by applying the sequential Bonferroni test (see Material and methods). (*) = $p \le 0.10$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

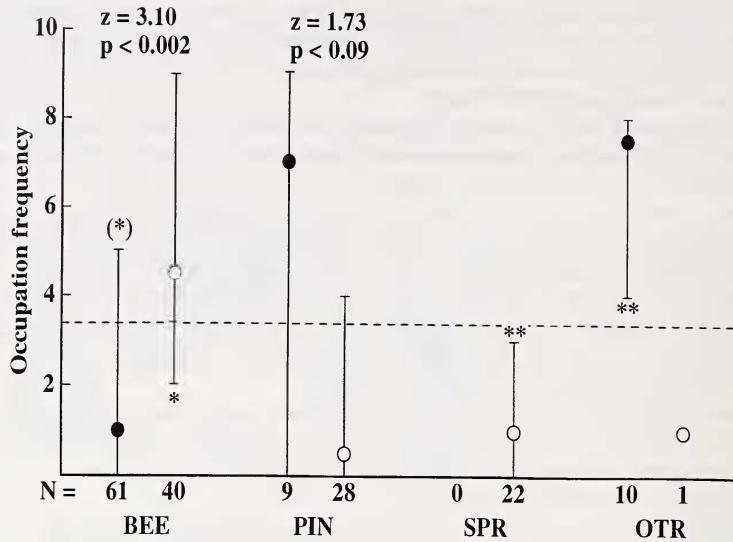| | coniferous-mixed forest | | deciduous forest | |
	small scale r_s	large scale r_s	small scale r_s	large scale r_s
BEE	0.06	0.12	–0.13	0.02
OAK	0.02	0.24	0.13	0.50**
PIN	–0.05	0.17	0.29	0.70**
SPR	–0.17	–0.20	–	0.40**
LAR	–0.05	–0.01	0.08	0.59**
OTR	–0.02	0.08	0.38**	0.58**
FRT	0.06	0.10	–0.03	–0.18
DIV	0.00	0.02	0.46**	0.76**
DEN	–0.14	0.13	0.21	0.60**
AGE	–0.13	–0.18	–0.43**	–0.50**
UST	–0.15	–0.56**	0.14	–0.05
YTR	0.10	0.17	0.26	0.17
TST	–0.16	–0.37**	0.27	0.77**
HDG	0.00	–0.07	–0.05	–0.38**
OPA	0.12	–0.09	0.05	–0.27
HIG	0.07	0.46**	–0.08	0.06
CIR	–0.07	0.43**	–0.07	–0.24
DIS	–0.17	0.10	0.16	0.33*
SUN	–0.14	0.27	–0.30(*)	–0.59**

Fig. 4. Occupation frequency of nest boxes (median and quartiles) attached to different tree species in the deciduous (●) and coniferous-mixed forest (○). The dashed line shows mean occupation frequency per nest box. Tests between forests are Mann-Whitney-U and difference from mean occupation frequency are t-test or signed rank test (SAS 1987). For abbreviations see Material and methods.
(*) = p ≤ 0.1; * = p < 0.05; ** = p < 0.01.

Small scale; deciduous forest:

In the deciduous forest correlations between nest box occupation frequency and habitat parameters revealed a significant preference for other trees and high tree diversity. Old tree stands and nest boxes with high sun exposure were avoided (Tab. 2).

The first 5 PC-axes accounted for 61.5% of the variation. The first axis (28.9%) and the fifth axis (6.4%) describing nest box parameters correlated significantly with occupation frequency (Fig. 6). In the first axis pine trees, larch trees, other trees, high tree diversity and density were preferred, whereas old tree stands were avoided (p < 0.0001). In the fifth axis, however, fruit trees and nest boxes with high sun exposure were avoided and understory cover was preferred (p < 0.006; Fig. 6). 61 of 80 nest boxes were attached to beech trees (76%), 11% of the nest box trees were pines and 13% were other trees. Nest boxes on beeches were occupied below mean occupation frequency, whereas nest boxes
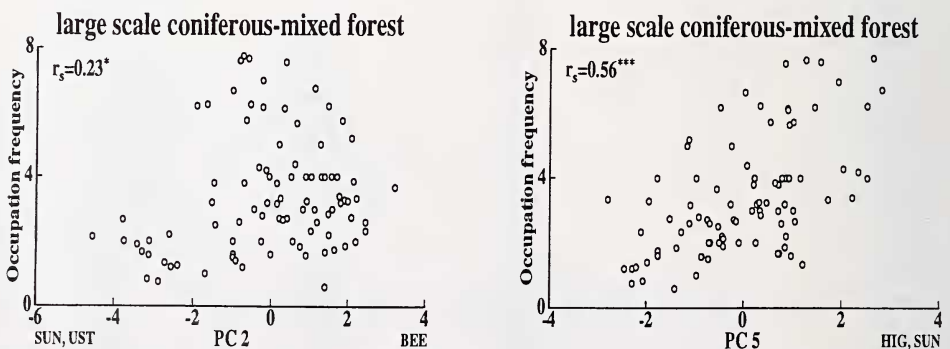

Fig. 5. Nest box occupation in relation to PC-axis 2 and PC-axis 5 in the large scale analysis of the coniferous-mixed forest. For abbreviations see Material and methods.

on other trees were significantly preferred (Fig. 4). The height of the nest boxes attached to beeches did not correlate with occupation frequency ($r_s = -0.19$). The same is true for pine ($r_s = 0.02$) and other trees ($r_s = 0.46$).
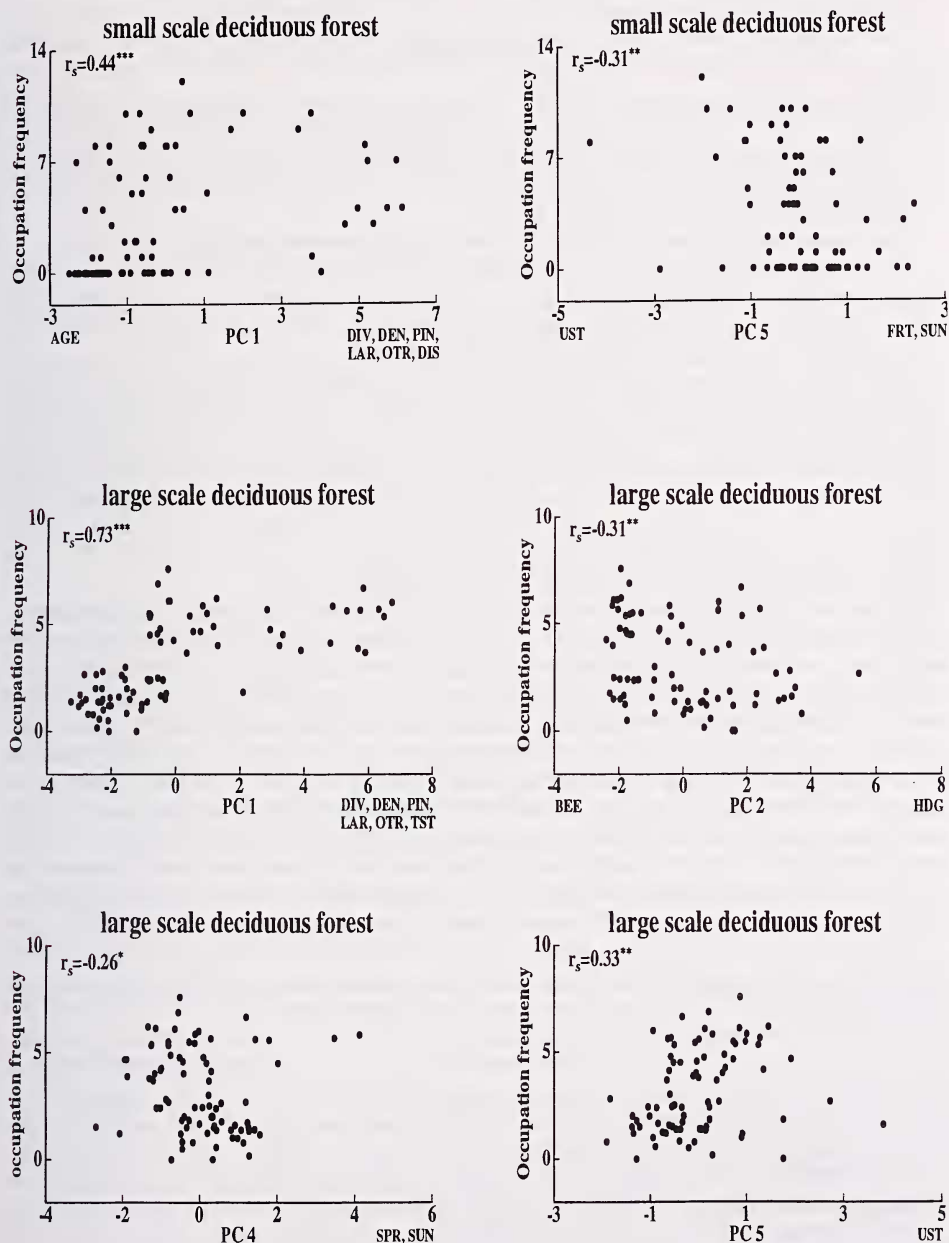

Fig. 6. Nest box occupation frequency in relation to PC-axis 1 and PC-axis 5 in the small scale analysis of the deciduous forest and in relation to PC-axes 1, 2, 4, and 5 in the large scale analysis of the deciduous forest. For abbreviations see Material and methods.

Large scale; deciduous forest:

In the large scale analysis areas with high tree diversity along with oak trees, pine trees, spruce trees, larch trees and other trees, high tree density and tree stumps showed positive correlations with mean occupation frequency, whereas old tree stands, nest boxes with high sun exposure and forest edge were negatively correlated (Tab. 2).

The first five PC-axes accounted for 81.4% of the variation. PC-axes 1, 2, 4 and 5 correlated significantly with nest box occupation (Fig. 6). The first axis (38.2%) describing high tree diversity with pine trees, larch trees and other trees and tree stands with high density, correlated positively. Moreover, areas with tree stumps were preferred (p < 0.0001). The second axis (18.0%) is characterized by preference for beech trees whereas forest edge was avoided (p < 0.006). In axis 4 (6.9%) spruce trees and nest boxes with high sun exposure were avoided (p < 0.03) and in axis 5 (5.1%) areas with a marked understory cover were preferred (p < 0.003).

Site fidelity and choice of nest boxes of individually marked animals:

From 1993 to 1995 more than 400 animals were marked in both forests. In 1993 not a single juvenile was observed in any of the two woodlands. Possible reasons for this complete absence of reproduction are discussed by BIEBER (1995) and SCHLUND (1996). In 1994 and 1995, however, the dormice did reproduce.

Emigration rates/death rates amounted to more than 50% in both forests between 1993 and 1994 (deciduous (dec): 64.2%; coniferous-mixed (con): 50.8%) and to more than 70% between 1994 and 1995, respectively (dec: 71.1%; con: 71.2%). In three years only 2 dormice migrated between the two woodlands (1 from dec to con, 1 vice versa). In 1995 the retrapping rate of juveniles born in 1994 was more than 25% in both woodlands (dec: 26.9%; con: 25.6%) and did not differ significantly from retrapping rates of adult dormice (31% in both woodlands; dec: $\chi^2 = 0.44$, df =1, n. s.; con: $\chi^2 = 0.43$, df = 1, n. s.). This indicates a preference for the woodland in which an animal was born.

Strong site fidelity becomes apparent by analysing nest box choice of gestating females in 1994 and 1995. Occupation rate of the nest boxes in which the females gave birth (dec: 41 females; con: 31 females) correlated with the number of nest boxes occupied in the last 13 years in both forests (dec: $r_s = 0.43$, p < 0.002, n = 49; con: $r_s = 0.25$, p < 0.05, n = 65). Furthermore out of 7 females that gave birth both in 1994 and 1995 in the deciduous forest, 5 did so in the same nest box and 2 changed to neighbouring nest boxes (distance 30 m). Likewise, in the coniferous-mixed forest 6 out of 8 females remained in the same nest box, 1 occupied the directly neighbouring nest box and 1 stayed in the near vicinity (67 m). Even the offspring of 1994 were still recorded close to their natal nest boxes in the following year. In the deciduous forest the mean distance was 61 m (n = 15), in the coniferous-mixed forest it amounted to 157 m (n = 6). The difference between forests as well as the difference between sexes was highly significant (Tab. 3), the

Table 3. Mean distance [m] between natal nest box (1994) and nest boxes where the sons and daughters were encountered in 1995.

	deciduous forest				coniferous-mixed forest			
	$\overline{x}$	Min	Max	n	$\overline{x}$	Min	Max	n
sons	106	60	160	5	321	162	480	2
daughters	38	0	133	10	75	0	154	4
2-way analysis of variance		F				p		
model		8.53				0.002		
woodland		11.41				0.004		
sex		17.66				0.0006		
woodland * sex		5.70				0.03		

daughters occurring consistently closer to their natal nest boxes than the sons. Daughters that became mothers in their first year, however, were found at similar distances as non-reproductive daughters (dec: mothers $\bar{x}$ = 44 m, n = 4; non-mothers $\bar{x}$ = 35 m, n = 6; t-test: t = 0.3, n. s.; con: mothers $\bar{x}$ = 100 m, n = 3; non-mother $\bar{x}$ = 0 m, n = 1, no test).

Discussion

In this long term study on nest box occupation by edible dormice we showed that the number of occupied nest boxes throughout 13 years was similar in both investigated woodlands, a deciduous and a coniferous-mixed forest. This does not agree with other studies reporting on deciduous forests as optimal habitats for this small mammal species being inhabited by more dormice than coniferous forests (STORCH 1978; HÖNEL 1991). However, a three year study (1993 through 1995) in the two forests on individually tagged edible dormice (passive integrated transponder) revealed a higher population density in the deciduous forest (SCHLUND 1996). Reasons for this discrepancy are: at first, one single nest box with a characteristic leaf nest may be occupied by up to 9 dormice (our own observation), secondly, other dormice may live in natural tree holes that are probably more common in the deciduous than in the coniferous-mixed forest. This means that the number of occupied nest boxes does not reflect population density. However, as this study shows, the analysis of occupied nest boxes through 13 years is sufficient to make statements on habitat utilization. Furthermore, frequently occupied nest boxes correlate with those nest boxes that are chosen for rearing young.

Habitat and site fidelity

Throughout the investigated 13 years the proportion of occupied nest boxes between the two forests remained relatively constant. Even in years with low density the coniferous-mixed forest was not vacated in favour of the better habitat. The forests are only 1 km apart and our radio-telemetry studies showed nightly ranges of dormice to the extent of more than 1 000 m (unpubl. data). Nevertheless exchange between the investigated areas was extremely rare. Thus, choice for woodlands is not made by assessing ad hoc qualities, although the perceptual range of dormice seems sufficiently large (see LIMA and ZOLLNER 1996). Forest utilization might be a result of tradition. A further indication is the high number of dormice being born and staying in the area where they have been raised (e. g. habitat preference in mice as a function of prior experience, ANDERSON 1973). This habitat fidelity is surprising since habitat quality even influences the condition of dormice. In the deciduous forest adult animals had higher body mass and larger body sizes, and reproductive output was significantly higher than in the coniferous mixed-tree forest (SCHLUND 1996; SCHLUND and SCHARFE 1996). Comparable results of optimal habitats influencing the fitness of animals are reported in studies on white-footed mice (WOLFF 1993) and red squirrels (WAUTERS and DHONDT 1989) and are explained by the authors with the more favourable food situation.

In addition, in either forest certain nest box areas were occupied more frequently than others, revealing a clumped dispersion. This strongly indicates that within both forests some areas were more suitable to edible dormice than others. The majority of occupied nest boxes were used for more than 8 years. Since the average life expectancy of dormice in the wild is 3 to 4 years (BIEBER 1995) preferences for specific areas exist over generations of animals. Contrary to PILASTRO (1992) we never found communal nesting in breeding females. However, we could demonstrate that female kin tend to stay and give birth in their natal nest box or in close vicinity.

Further aspects refer to sex and habitat specific dispersal differences. In both forests

females stay closer to their natal nest box than their brothers suggesting male dispersion (a common behaviour in mammals; GREENWOOD 1980; e. g. GOUNDIE and VESSEY 1986). In the coniferous-mixed forest both male and female offspring are found at greater distance from their birth place than in the deciduous forest. This may be due to differences in habitat quality and therefore divergent food resources of the two forests. The low quality coniferous-mixed forest might induce an expansion in individual foraging range, or wider dispersal to favourable but patchily distributed feeding areas (WAUTERS et al. 1995; see also WINKER et al. 1995).

Habitat utilization

Correlations between nest box occupation and habitat parameters differed considerably between the two forests. Corresponding to these differences in habitat characteristics, completely different parameters were obviously important for the utilization of the optimal habitat. Hence, edible dormice followed no rigid choice pattern.

As a result of the strong site fidelity of edible dormice we might have expected that dormice exhibit habitat preferences on the small scale, meaning the areas directly around a nest box ($900\,m^2$). However, on the level of the small scale habitat choice seems to play a secondary role. In the coniferous-mixed forest edible dormice did not show preferences for any of the habitat parameters. The choice for nest box trees, however, was clearly a choice for beeches. In a forest consisting mainly of pine and spruce, this could be interpreted as a behavioural reaction of an animal that is mostly attached to deciduous trees. In the deciduous forest beeches as nest box trees were rather avoided whereas other deciduous tree species were selected. A fact that might be attributed to the smooth and slippery bark of old beeches with large circumference, where dormice might easily slip and fall (LÖHRL 1960; v. VIETINGHOFF-RIESCH 1960; SCHOPPE 1975). This is in contrast to the coniferous-mixed forest where beeches are younger with smaller circumferences and branches growing lower at the tree trunk and are thus easier to climb. Furthermore, in the small scale analysis of the deciduous forest, preferences for few habitat parameters occurred. The importance of these parameters is elucidated on the large scale analysis.

Edible dormice live predominantly on a vegetarian diet consisting mainly of leaves in the early summer and fruits rich in protein and edible (e. g. oak and beech trees) in the autumn (v. VIETINGHOFF-RIESCH 1960; STORCH 1978). This accounts for the finding that on the large scale ($8\,100\,m^2$) the animals are found in areas with rich food sources meaning areas with oak trees and beech trees. Furthermore, in the deciduous forest they utilized areas with high tree diversity. Tree species like ash, lime or maple as well as pine and larch are an important enrichment in diet (EIBERLE 1977; HÖNEL 1991; KULZER et al. 1993). In the coniferous-mixed forest deciduous tree species were extremely rare with the exception of beech trees. Therefore beeches were preferred. Taking this relatively unbalanced diet of beeches into consideration, it seems surprising that edible dormice avoided nest box areas with a marked understory cover that consisted mainly of blackberries and raspberries. As our telemetry studies showed (unpublished work), dormice did indeed feed on blackberries and raspberries. However, since nest box areas with a high proportion of beech trees were preferred and since those correlated with low sun exposure on the ground, understory cover was not developed there.

Besides food availability predator avoidance may explain differences in habitat utilization. Both investigated forests are hunting grounds of the tawny owl (*Strix aluco* L.). This species catches its prey preferably in flight e. g. dormice while they are foraging in the tree crown. Dense areas provide the best protection against this predator (see BEZZEL 1985). In the heterogeneous deciduous forest where dense young tree stands alternate with old and open areas edible dormice preferred indeed the denser tree stands. This is

not true for the coniferous-mixed forest. In this more homogeneous forest dense stands of deciduous tree species are nearly non existent, with the exception of stands of spruce trees which, however, are avoided.

Further protection against the tawny owl may be given by nest boxes fixed higher up on trees reducing the exposed and thus risky way between nest box and foraging place in the tree crown. In the coniferous-mixed forest nest boxes attached higher up were preferred. In the deciduous forest a comparable behaviour does not seem to exist. Here, height of the nest box does not correlate with occupation frequency. This is attributed to the tall beeches which account for 76% of the nest box trees. Here branches providing footholds or protection to the dormice on their long way (up to 15 m) to and from the tree crown do not exist. Thus a reduction of the distance between nest box and tree crown by a maximum of 1 m can not reduce the risk of predation or of slipping. This even forced the dormice to enter their nest boxes via neighbouring bushes or the ground (pers. observ.). In the coniferous-mixed forest the distance between nest box and tree crown is smaller and branches are found all the way down to the nest box, a result of different forest management.

Cats often catch edible dormice, as many residents of Hagelloch, the village bordering directly on the deciduous forest, reported. This hunting success is facilitated by dormice using the ground to access nest boxes at beech trees. Furthermore the abundance of cats from the nearby village might be a reason why dormice avoid the forest edge in the deciduous forest. This is a completely contrary result to an other study that has shown preferences of edible dormice for forest edges (BIEBER 1995) due to a higher quality e. g. higher availability of food resources than inside the forest. In our investigation area, however, the food supply is guaranteed by intense fructification of many old oak trees and beech trees in the forest interior. In contrast, in the coniferous-mixed forest without adjacent settlement of men we found no avoidance of the forest edge. No positive edge effect could be observed, either. This might be due to less marked forest edges with only few and sparsely grown hedges.

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Zusammenfassung

Habitattreue und Habitatnutzung von Siebenschläfern, Myoxus glis (L.), in zwei unterschiedlichen Wäldern

In einem Laubwald und einem Nadel-Laubmischwald wurden über 13 Jahre (1982–1994) Nistkastenbelegungen durch Siebenschläfer untersucht. In beiden Waldgebieten gab es Areale, die von Siebenschläfern bevorzugt, andere dagegen gemieden wurden. Nur wenige Tiere wechselten zwischen den Gebieten, obwohl diese nur einen Kilometer auseinander lagen. Auch innerhalb der Waldgebiete war die Standorttreue der Siebenschläfer um bestimmte Nistkästen hoch, wobei im Laubwald die Nistkastentreue höher als im Nadel-Laubmischwald war. Außerdem zeigten Mütter und ihre Töchter höhere Nistkastentreue als Männchen. In beiden Waldgebieten wurden auf zwei räumlich unterschiedlichen Maßstäben (900 m^2 und 8 100 m^2 um jeden Nistkasten) die Nistkastenbelegungen mit 19 Habitatvariablen korreliert. Diese Korrelationen unterschieden sich zwischen den Waldgebieten erheblich, führten aber in beiden Gebieten zum gleichen Resultat: Auf der Ebene des großen Maßstabs waren Faktoren zur Nahrungssuche (z. B. Buchen, Eichen) und zum Prädationsschutz (z. B. Baumdichte, Nistkastenhöhe) wichtig. Auf der Ebene des kleinen Maßstabs spielte die Habitatwahl der Siebenschläfer nur eine untergeordnete Rolle.

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